

Rates of post-larval bedload dispersal in a non-tidal soft-sediment system

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ABSTRACT: Quantifying rates of dispersal and understanding patterns of colonization are key for predicting disturbance–recovery dynamics. For soft-sediment benthic communities recruitment is not restricted to one single event, but can be highly variable on several spatial and temporal scales. To investigate the temporal persistence of post-larval bedload transport in a non-tidal system, field experiments were conducted at 4 sites (5 m depth) across a wind-wave exposure gradient over 2 summers. Results indicate that bedload dispersal is temporally variable and dependent on an interaction between species-specific characteristics (including seasonal peaks in reproduction), site-specific hydrographic conditions, grain size characteristics and transport of sediments and drift algae. Dispersal of more passive taxa (Ostracoda, juvenile gastropods, *Macoma balthica*) was found to be associated with higher rates of sediment and algal transport, while more active species (*Hydrobia ulvae* and *Potamopyrgus antipodarum*) dispersed relatively more at sheltered sites. At higher rates of sediment transport, there was an increase in the proportion of larger *M. balthica* individuals dispersing, in contrast to Hydrobiidae, which had an increased proportion of smaller individuals. Our study suggests that frequent post-larval dispersal plays a central role in the population dynamics of many benthic invertebrates, in non-tidal systems. While the distribution of species is heavily influenced by peaked larval recruitment over large spatial scales, the net result of continuous small-scale dispersal events is clearly important and may contribute to the resilience of benthic communities.

KEY WORDS: Invertebrate · Benthos · Baltic Sea · Mobile · Recruitment · Connectivity

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INTRODUCTION

Rates of dispersal and patterns of colonization are key for understanding disturbance–recovery dynamics and assessing resilience in ecological communities. Nevertheless, in marine ecosystems, dispersal and colonization processes are still poorly known (Cowen & Sponaugle 2009). The relative contribution of local, regional, or global dispersers has profound implications for community dynamics and resilience to disturbance (Palmer et al. 1996, Whitlatch et al. 1998, Thrush et al. 2009). Despite the global dispersal potential of many species, short-dispersing fauna are also common, especially in soft-sediment ecosystems

(Grantham et al. 2003). It was previously assumed that recruitment patterns mainly reflect patterns of regional larval supply and settlement at a large-scale (Thorson 1950, Becker et al. 2007). However, dispersal and subsequent recruitment have been found to be highly variable on several spatial and temporal scales (Günther 1992, Armonies 1994, Palmer et al. 1996, Snelgrove & Butman 1994). Recruitment into benthic communities is not restricted to one single event but is continuous and depends on the sum of all dispersers reaching a site over time and subsequent survival. Dispersal at the post-larval stage can, for example, provide the opportunity for frequent smaller-scale movement, enhancing exchange of individuals be-

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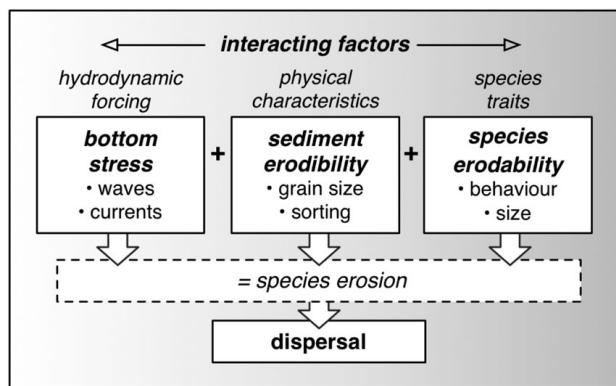


Fig. 1. Combination of factors required to maintain bedload dispersal. Hydrodynamic forcing together with local sediment characteristics interact with species-specific traits to initiate species erosion and subsequent dispersal

tween sub-populations (e.g. Norkko et al. 2001), but is often highly variable depending on local conditions (Cummings et al. 1995, Lundquist et al. 2006). Dispersal also depends on species-specific differences in reproductive modes and development, which can play a vital role in local population fluctuations (Thorson 1950, Ólafsson et al. 1994). High rates of post-larval dispersal have been recognized as important in the recolonization process in response to disturbance, especially small-scale disturbances (Whitlatch et al. 1998), and their contribution to higher resilience in benthic communities (Cummings & Thrush 2004, Thrush et al. 2008, Norkko et al. 2010).

Rates of sediment transport and the subsequent dispersal of benthic fauna in the bedload are closely related to the amount as well as type of energy reaching the bottom in combination with site-specific conditions (Fig. 1, Norkko et al. 2002, Le Hir et al. 2007). For wave-dominated tidal systems, both waves and currents are regularly superimposed across large intertidal areas. Regularly during flood and ebb tide, the potential for bottom shear stress to exceed thresholds for erosion is non-linearly enhanced (Le Hir et al. 2007). Also in the absence of waves, regular fluctuations in bottom shear stress in strong tidal systems can increase the opportunity for bedload dispersal and provide for frequent small-scale dispersal events that are important community-structuring mechanisms (e.g. Beukema & de Vlas 1989, Emerson & Grant 1991, Thiébaut et al. 1998). In these systems, post-larvae have been reported to not only disperse as bedload but also regularly enter the water column to be dispersed (Commito et al. 1995a, Cummings et al. 1995). However, our knowledge of post-larval dispersal potential is very limited for non-tidal systems, for example in the Baltic Sea, where quantitative information on rates of bedload dispersal is exceedingly scarce (Norkko et al.

2010, Valanko et al. 2010). The absence of regular tides would suggest that sediment erosion is a more stochastic event and dependent on wind-induced currents and waves exceeding a long-term average (at a constant depth) (Soomere 2008). It is not known whether these stochastic peaks in the oscillatory flow components are strong enough to initiate, or regular enough to maintain, rates of sediment bedload transport and subsequent post-larval dispersal. A lack of regular sediment bedload transport may have implications for the connectivity and resilience of benthic communities. Nevertheless, a previous study has shown that a significant proportion (up to 40%) of taxa in a northern Baltic coastal soft-sediment community lack a planktonic larval life-stage, which would suggest that post-larval dispersal strategies play a significant role in structuring benthic communities also in non-tidal systems (Valanko et al. 2010).

Bedload transport, the movement of particles in continuous or near-continuous contact with the bed, is greatest at times when bottom shear stress (BSS) is sufficient to cause erosion (Le Hir et al. 2007). Species erosion and subsequent dispersal is modified by several interacting factors (Fig. 1). When species are not permanently attached to their substrate, erosion and transport of post-larvae in the bedload is an especially important process. Fluxes in post-larval bedload dispersal have been associated with wind-wave activity and sediment resuspension (e.g. Eckman 1983, Commito et al. 1995a, Lundquist et al. 2006). The presence of seasonal drift algae and its subsequent transport in the bedload can also increase the probability of dispersal by rafting by, for example, hydrobiont snails and other species associated with algae (e.g. Highsmith 1985, Norkko et al. 2000). However, rates of dispersal do not have a simple linear or monotonic relationship with BSS, but also depend on sediment erodability as well as species behavioral responses (Fig. 1). Especially for infaunal species, an ability to burrow or emerge can be an important mechanism in regulating erosion rates and subsequent transport along the bottom as bedload (Armonies 1988, Hewitt et al. 1997, Lundquist et al. 2004). With an increase in size, many infaunal species may burrow deeper and resist erosion, but as juveniles, they commonly inhabit the sediment surface and are more easily eroded (Fig. 1). In comparison, many epifaunal species disperse more actively. For example, the epifaunal Hydrobiidae may respond opportunistically to disturbance, rapidly aggregating around patches of food (drift algae, microphytobenthos; Norkko & Bonsdorff 1996, Herman et al. 2000).

In addition to species behavior, differences in site-specific grain-size characteristics may also affect rates of sediment erodability and transport (Fig. 1). Nel et al. (2001) found that burrowing rates in bivalves were

highest in well-sorted medium-grained sand, but that this relationship was bivalve size-dependent. Flume experiments have shown that finer sand and thus, the associated fauna, have lower critical erosion thresholds than coarser grained sand and fauna (Hunt 2004). Conversely, more cohesive sediments or sediments with a mud content >30 % behave differently: they are more consolidated and can have high erosion thresholds, comparable to medium sand or pebbles (Le Hir et al. 2007). Even changes in small-scale sediment surface topography, such as ripple formation, can have an effect on the resident community, with higher density and species richness in troughs, where shear stress is reduced (Ramey et al. 2009). Biotic interactions may directly affect sediment erodability by, for example, microphytobenthos producing protective films on the sediment surface (Paterson 1997), destabilization of sediment surface by bioturbation by organisms (de Deckere et al. 2001), organism-induced fluxes of sediment (Graf & Rosenberg, 1997), or the presence of organisms and macrophytes on or near the sediment surface changing bottom roughness (Nowell et al. 1981, Commito et al. 2005).

In a previous study we showed, using a range of different traps, that a variety of species-specific post-larval dispersal strategies occur, even in the absence of regular tidal-mediated currents (Valanko et al. 2010). We found bedload transport to be much more important than other modes of transport, such as water column transport; however, our previous short-term study (in October) did not quantify temporal variability of bedload transport. Variation in environmental variables can directly affect rates of bedload dispersal, which can further be modified by seasonality and species-specific characteristics (Fig. 1). To provide insight into the mechanisms of post-larval bedload dispersal, we conducted a mensurative field experiment at 4 sites in the northern Baltic Sea over 2 summers (7 sampling times). Rates of bedload dispersal are influenced by an interaction of abiotic and biotic conditions (Fig. 1). In this study, we predicted that dispersal rates (1) will depend on the amounts of sediment and algal bedload transport, (2) will be temporally variable, and (3) will exhibit species-specific responses that depend on the species life-history characteristics. In order to test these predictions, repeated sampling was carried out using sediment bedload traps. Traps were deployed by SCUBA at 4 coastal sandy sites, across a wind-wave exposure gradient from sheltered to exposed, which allowed for site-specific comparisons of disper-

sal patterns with respect to variation in local hydrodynamics and sedimentary conditions, as well as the resident community.

MATERIALS AND METHODS

Sampling. Study area: Four sandy sub-littoral sites (Sites A–D; Fig. 2) were chosen in close proximity to Tvärminne Zoological Station in south-western Finland ($59^{\circ} 50' N$, $23^{\circ} 15' E$). The depth of the sites was ~5 m (Table 1) with sediment surfaces varying from smooth to rippled, indicative of low to high-energy environments. Sites were chosen to span a gradient of increasing exposure to waves and wind from A to D.

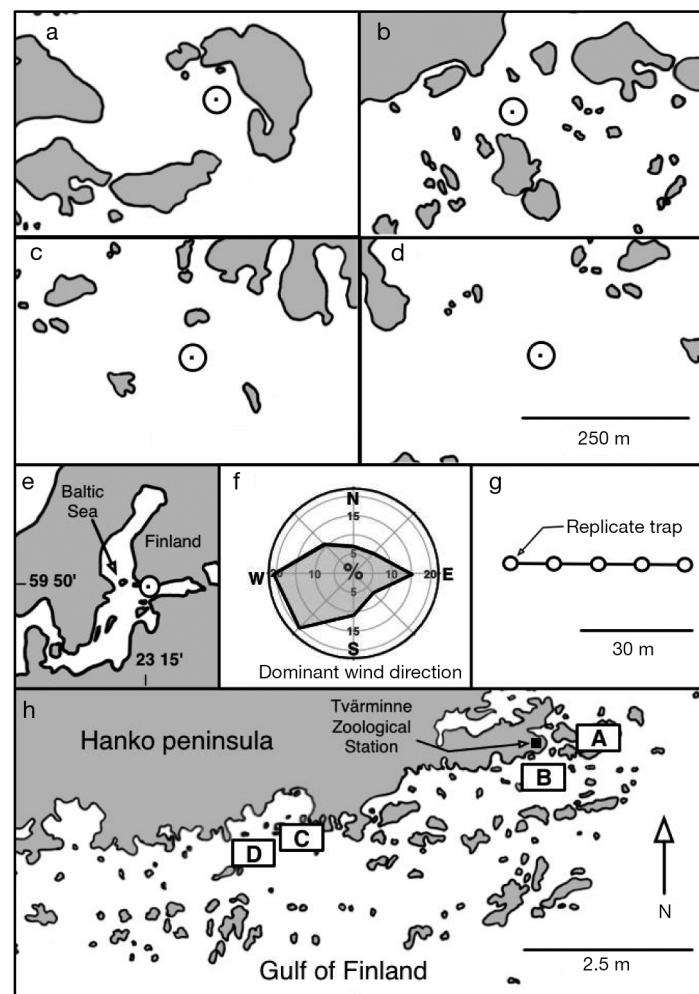


Fig. 2. Study sites and experimental design. (a) Site A, (b) Site B, (c) Site C, (d) Site D. (e) Hanko Peninsula in south-western Finland. (f) wind rose showing dominant (%) wind direction in summer 2006 and 2007 over the study period; (g) arrangement of replicates at each site; (h) study sites in relation to one another. Exposure to wind and waves increases from Site A to D

Table 1. Site-specific differences in abiotic conditions and dispersal. Depth (m) at sites; Exposure (calculated with a GIS-based wave exposure model developed by Isaeus 2004); Observed median grain size (d_{50}); Degree of scatter in grain size distribution (S_l); Percentage of sediment cohesive (<0.063 mm); Estimated friction velocity (u_*); Predicted critical friction velocity (u_{*crit}) (based on the Shields curve and calculated for corresponding median grain size). Site-specific mean relative dispersal rates of number of taxa and individuals. Site-specific ratios of dispersal associated with large transport of sediment ($>0.1 \text{ g d}^{-1}$) or algae ($>0.01 \text{ g d}^{-1}$). Ratios are presented for individual species abundances in respective traps, for total number of all ind. (absolute), number of ind. in relation to ambient abundance (relative) and total number (taxa). NA = undefined because of insufficient observations or 0 value in either the numerator or the denominator of the ratio calculation. VMR: variance–mean ratio

Site	A	B	C	D
Environmental conditions				
Depth (m)	5.8	4.0	5.7	4.2
Exposure	22156	22473	82371	88459
d_{50} (mm)	0.14	0.29	0.39	0.60
Sorting (S_l)	0.89	0.91	1.42	1.37
<0.063mm (%)	6.6	1.8	0.8	0.4
u_* (cm s $^{-1}$)	0.18	0.48	0.72	0.81
u_{*crit} (cm s $^{-1}$)	1.25	1.41	1.51	1.73
$u_{*crit} - u_*$ (cm s $^{-1}$)	1.07	0.93	0.79	0.92
Ambient community				
VMR ind. core $^{-1}$	9.8	8.3	7.8	8.4
VMR taxa core $^{-1}$	0.18	0.10	0.14	0.25
Dispersing community				
VMR ind. d $^{-1}$	3.7	17.4	56.6	118.6
VMR taxa d $^{-1}$	1.01	1.64	0.86	2.03
Relative dispersal				
Ind. d $^{-1}$	0.07	0.18	0.50	0.47
Taxa d $^{-1}$	0.49	0.61	0.72	0.62
Sediment associated dispersal				
Absolute	1.6	7.9	2.7	8.4
Relative	1.5	11.8	2.5	7.8
Taxa	1.4	2.1	1.4	2.3
<i>Macoma balthica</i>	8.0	NA	NA	NA
Ostracoda	1.1	8.6	4.8	14.0
Oligochaeta	1.3	NA	5.6	4.7
<i>Marenzelleria</i> sp.	NA	NA	0.1	0.2
Juvenile gastropod	1.5	1.4	1.6	5.2
<i>Hydrobia ulvae</i>	1.7	NA	0.7	1.5
<i>Potamopyrgus antipodarum</i>	1.1	14.8	0.5	0.5
Chironomidae	0.8	1.1	3.5	12.7
Algae associated dispersal				
Absolute	1.3	2.2	all >0.01g	6.4
Relative	1.4	2.0	–	6.4
Taxa	1.3	1.5	–	2.7
<i>Macoma balthica</i>	4.3	3.6	–	NA
Ostracoda	1.2	2.2	–	6.1
Oligochaeta	1.0	1.4	–	2.8
<i>Marenzelleria</i> sp.	NA	NA	–	0.3
Juv. gastropod	2.2	3.4	–	3.6
<i>Hydrobia ulvae</i>	1.9	1.2	–	3.3
<i>Potamopyrgus antipodarum</i>	0.9	2.9	–	NA
Chironomidae	1.9	1.7	–	NA

Relative exposure at each site was quantified using a GIS-based wave exposure model developed by Isaeus (2004). This model did not use bathymetric data, but shoreline coastal shape together with main wind direction (SW), and a maximum fetch distance of 500 km at a 25 m 2 grid resolution (Table 1). There are no regular tides in the Baltic Sea, so local currents are mainly wind induced and, at a larger scale, intrinsically barometric (Soomere et al. 2008). Over the summer sampling period May–October in 2006 and 2007, average wind speed was 6.8 m s $^{-1}$ mainly from a south-westerly direction (Fig. 2f; data from the Finnish Meteorological Institute weather station at Jussarö 59° 49' N, 23° 34' E and Russarö 59° 46' N, 22° 57' E).

Bedload dispersal: Sediment bedload traps were used to quantify rates of dispersal in relation to the ambient community on 7 different occasions in 2006 and 2007 (Appendix 1), with sampling times chosen to encompass different periods in the very seasonal recruitment patterns of benthic macrofauna in the northern Baltic Sea. At each of the 4 sites, 5 replicate traps were positioned along a 50 m transect (Fig. 2g). For each sampling occasion, traps were deployed on the same day (max. 5 h difference) at all sites over the same 48 h period using SCUBA. Samples for ambient community data were collected during the same period. Cylindrical traps (see Valanko et al. 2010 for more detail) were constructed from plastic pipe (\varnothing : 3.7 cm, depth: 29 cm) with an aspect ratio of 7.8:1. The traps were slotted into a pre-deployed outer sleeve, and a rubber gasket kept the trap in the outer sleeve and flush with the sediment surface. Before being submerged, bedload traps were filled with seawater and sealed with rubber stoppers. Upon deployment, stoppers were removed, and reinserted before recovery of the traps in order to keep the samples intact.

Resident benthic community: Ambient community composition was sampled by taking triplicate cores (\varnothing : 5.6 cm, depth: 15 cm) at trap positions 1, 3 and 5 at each site. Average ambient community abundances were first calculated per position ($n = 3$) and then for each site and time.

Sample preservation and analysis: All samples were preserved in 70% ethanol and stained with rose Bengal for later analysis. Trap samples were sorted and enumerated using a binocular microscope. An elutriation and decanting technique was applied prior to sorting of ambient community samples, which contained large amounts of coarse sediment. The preserved sample was washed into a bucket that was gently agitated by adding water while applying a swirling action, bringing lower mass animals and organic material into suspension. Suspended material was then decanted through a 0.2 mm sieve to include post-larvae of macrofaunal species in the area. This was repeated 5

times until no more animals were decanted. The sieve content was sorted under the microscope. Remaining sediment was sieved through a 0.5 mm sieve and visually inspected on a tray for potential larger, heavier animals that were not separated from the sediment by elutriation.

Sediment and algal transport: During sorting of bed-load trap content, animals, sediment and algal/plant material (mainly filamentous macroalgae and seagrass) were separated. Subsequently, dry wt of sediment and algal material was determined separately (48 h at 60°C), and expressed as g d⁻¹. When sediment erosion occurs, rates will increase exponentially with increased bottom shear stress (e.g. Houwing 1999). We therefore expressed increases in both sediment and algal transport rates on a logarithmic scale.

Granulometric analysis: Sediment grain size was determined from 5 replicate cores (\varnothing : 2.1 cm, depth: 5.0 cm) collected one from each trap position at each site and frozen for subsequent analysis. Hydrogen peroxide (H_2O_2 , 6%) was used to dissolve organic material. Grain sizes were separated into <0.063, >0.063, >0.250, >0.500, and >2.00 mm size class fractions using respective sieves. Dry wt (48 h at 60°C) was obtained for each grain size class. Percentage finer than each consecutively larger size fraction was calculated. Sieve mesh sizes (mm) were converted to the phi scale (F):

$$F = -\log_2 (\text{mm}) \quad (1)$$

(Folk & Ward 1957). Cumulative percentages were plotted against F values for each sample separately. Median grain size (d_{50} mm) was determined for each sample, from which a mean ($n = 5$) was obtained for each site. The amount of scatter in sediment grain size distribution can be used to describe the type of energy at the site, with well-sorted sediment indicative of more consistent energy. Degree of sorting (S_I) was obtained from each individual samples' cumulative percentage plotted against their F value. The mean inclusive graphic standard deviation was calculated as:

$$S_I = \frac{F_{84} - F_{16}}{4} + \frac{F_{95} - F_5}{6.6} \quad (2)$$

for each site (Folk & Ward 1957).

Hydrographic measurements: Critical values for initiation of transport were calculated using the median grain size at each site. Initiation of sediment transport was estimated using the threshold Shield parameter (I_{crit}) improved by Soulsby & Whitehouse (1997):

$$\theta_{crit} = \frac{0.3}{1+1.2D_*} + 0.055[1-\exp(-0.02D_*)] \quad (3)$$

where D_* is a dimensionless grain size. Dimensionless grain size is defined as:

$$D_* = \left[\frac{g(\rho_s/\rho_w)}{v^2} \right]^{1/3} d \quad (4)$$

where g is the acceleration due to gravity, ρ_s and ρ_w are the sediment and water densities, v is the kinematic viscosity of water and d is the grain diameter (Soulsby 1997). Predicted site-specific critical bed shear stress τ_{crit} was calculated using the equation:

$$\tau_{crit} = \theta_{crit} g(\rho_s - \rho_w) d \quad (5)$$

and corresponding predicted critical friction velocity as:

$$u_{*crit} = \left(\frac{\tau_{crit}}{\rho_w} \right)^{1/2} \quad (6)$$

(Soulsby 1997). To determine the relative difference in hydrodynamic conditions between sites, a gypsum dissolution technique was used, which is a method that has been successfully applied in combination with dispersal traps in other field studies (e.g. Yund et al. 1991, Committo et al. 1995a). Replicate gypsum blocks (\varnothing : 4.5 cm, height: 2 cm) were deployed for 48 h at each site using metal rods inserted into the sediment. At each of the 5 sampling blocks, 1 gypsum block was deployed at 30 cm height (i.e. close to the bottom but still avoiding contact and abrasion). At the time of deployment (9–11 October 2007), average wind speed was 8.4 m s⁻¹ with peak gusts of up to 13 m s⁻¹ from a westerly (296°) direction. Gypsum blocks were weighed before and after deployment, after being oven dried for 48 h at 60°C. Differences in relative current and wave energy between sites were determined from the change in dry wt. Site-specific changes in dry wt of gypsum blocks was related to an *in situ* calibration study between gypsum blocks and direct turbulence measurements, using an acoustic Doppler velocimeter (ADV) with a sampling frequency of 16 Hz (Oikkonen et al. unpubl.). These measurements were conducted at Sites A–D and an additional 11 sites at ~5 m depth to span a larger range of exposure with wind (mean: 6.9 m s⁻¹, peaks of 11.4 m s⁻¹) from the dominant direction (211°). A good correlation (0.98) between ADV measurement (3 × 20 min) and gypsum lost over 48 h was established. This provided an accurate estimate of site-specific friction velocity for Sites A–D of the current study, and enabled a comparison to the site's critical values of initiation of sediment transport (i.e. the smaller the difference the more likely sediment transport was at the site).

Data analysis. Rates of dispersal: All trap data was standardized to 24 h. Traps that contained >10 g sediment or >0.4 g algae trap⁻¹ d⁻¹ ($n = 17$) were deemed not to have worked optimally over the whole sampling period, as the aspect ratio of the traps would have changed, and were consequently removed prior to analysis (no. of traps used was: A = 35, B = 32, C = 22,

$D = 34$). Spatial and temporal variation in absolute dispersal was examined for total abundance and number of taxa using a fixed factor 2-way ANOVA with site and time as factors. Prior to analyses, data was log transformed to meet the assumptions of normality and homogeneity of variances. Eight taxa were chosen for further analysis, representing the most abundant taxa in the ambient community and in traps, across all sites and times. These taxa collectively accounted for a total of 91.5 % of ambient and 95.3 % of dispersing individuals. Dispersal rates were then calculated separately for each taxon in 2 different ways (see Commito et al. 1995b, Turner et al. 1997, Commito & Tita 2002). Absolute dispersal rate = number of individuals (ind.) trap $^{-1}$ d $^{-1}$. Relative dispersal rate = number of ind. trap $^{-1}$ d $^{-1}$ /(ambient ind.), which is the number of ind. trap $^{-1}$ captured during 24 h deployment, divided by corresponding ambient mean number of ind. core $^{-1}$. In situations when a species recorded in a trap had a corresponding average ambient density <1 , relative rates tended to infinity and the observation was thus removed from the analysis. Species-specific seasonality was calculated using average absolute dispersal rates across the 4 sites at 3 different sampling occasions (in May, July, and October) of 2007. On each occasion, taxa proportions (%) of total from all 3 occasions were determined.

Variance-mean ratio (VMR): Changes in VMR can be a useful indication of change across spatial and temporal scales and can also be useful when comparing species that occur at different abundances (e.g. Hewitt & Thrush 2009). This measure of homogeneity in distribution was calculated for both ambient abundance and absolute dispersal rates. VMR was used to compare total number of taxa and individuals, as well as taxa-specific, patterns across times and sites.

Sediment and algal associated transport: In order to gauge whether a taxon was associated with fluxes of sediment, its average abundance in traps that had caught >0.1 g sediment d $^{-1}$ was compared to its average abundance in traps that had caught <0.1 g sediment d $^{-1}$ and expressed as a ratio. Similarly, to evaluate whether a taxon was associated with fluxes of algae, its average abundance in traps that had caught >0.01 g algae d $^{-1}$ was compared to its abundance in traps that had caught <0.01 g algae d $^{-1}$ and expressed as a ratio. Ratios for total number of dispersing taxa, and total absolute and relative rates of dispersal, were also calculated for both sediment and algal associated transport.

Thresholds in site-specific dispersal rates: In order to investigate generality in bedload dispersal rates across time and space in a multi-species context, changes in mean relative rate of dispersal as well as in upper quantiles (0.90 and 0.99) of the mean were used to explore be-

tween-site differences with changes in amounts of algal and sediment transport. Four classes of consecutively larger amounts of transport were defined on a logarithmic scale for sediment ($0.001\text{--}0.01$, $0.01\text{--}0.1$, $0.1\text{--}1$, and $1\text{--}10$ g d $^{-1}$) and algae ($0.0001\text{--}0.001$, $0.001\text{--}0.01$, $0.01\text{--}0.1$, and $0.1\text{--}1$ g d $^{-1}$). All species relative rates >0 were used to calculate means and upper quantiles (0.90 and 0.99) in traps within each predefined sediment and algal class, which were then used to fit a line and plotted on top of actual data for each site. In a multi-species context, it is expected that changes in relative bedload dispersal rates will occur at different times with increased algal or sediment transport, depending on species as well as site-specific conditions. A situation with no changes in the mean but a sudden increase in variation indicated by the upper-boundary conditions (0.90 and 0.99 quantiles) can be interesting (e.g. Cade & Noon, 2003) as it is indicative of a response to higher rates of sediment or algal transport.

Size-dependent dispersal: Size-dependent dispersal with increasing sediment transport was addressed for the bivalve *Macoma balthica* and the gastropod group Hydrobiidae, which exhibited contrasting dispersal strategies (within the constraints of the methods and scale of this study). All traps from all sites and all times were divided into one of 4 classes on an increasing log scale according to how much sediment they had caught (g sediment d $^{-1}$). A non-parametric Mann-Whitney test was used to compare the median sizes of individuals, and a 2-sample Kolmogorov-Smirnov test was used to test differences in size-frequency distribution between ambient and the different amounts of sediment transport.

RESULTS

Spatial and temporal variation in dispersal

Our study area exhibited strong seasonality in temperature, with a maximum of 20.1°C in August and a minimum of -0.1°C in March, and 53 d of ice cover in February and March. Average monthly wind conditions were reasonably consistent, with highest monthly mean in December (10.4 m s $^{-1}$) and lowest in July (5.9 m s $^{-1}$). Two day average wind conditions measured during sampling occasions were highest in August (10.8 m s $^{-1}$) and lowest in May (5.6 m s $^{-1}$) (Fig. 3). However, both the total abundance and number of taxa of the dispersing community were highly variable in time and space (Fig. 3 and see Appendix 1). On most sampling occasions, both the number of individuals and taxa in the dispersing community were highest at Sites C and D in comparison to Sites A and B. For total community dispersal, there was a significant effect of site

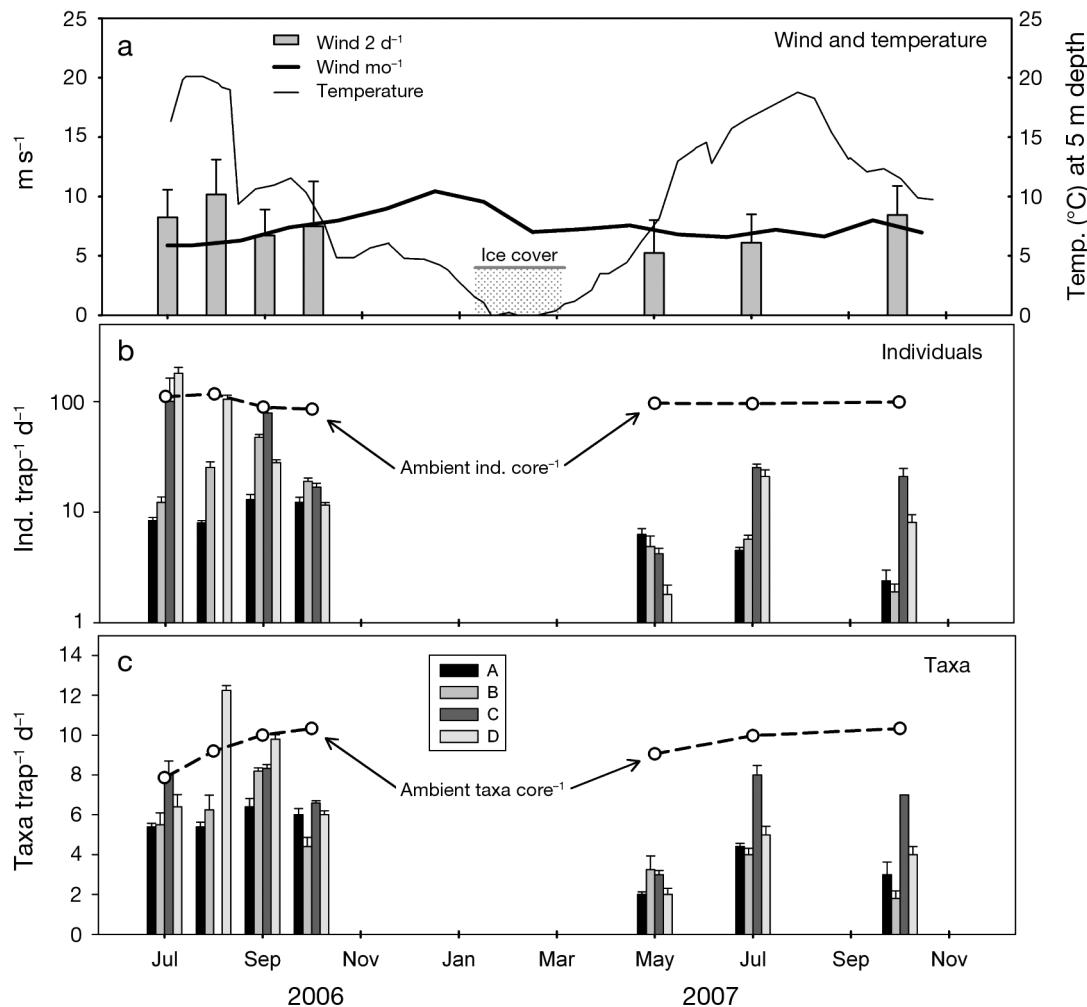


Fig. 3. Seasonality in abiotic condition. (a) Monthly mean wind speed with 2-day means (\pm SD) at the time of sampling, water temperature at 5 m depth and the extent of the ice cover period. (b,c) Site-specific (A–D: bars) temporal variability in absolute number (mean \pm SE) of dispersing individuals (ind.) and dispersing taxa, respectively, along with mean numbers of ind. and taxa in the ambient community (dashed lines)

(fixed factor 2-way ANOVA; $F_{3,61} = 21.9$, $p < 0.0001$) and time ($F_{3,61} = 63.2$, $p < 0.0001$) on total dispersal. This was also seen for number of taxa with site and time being significant ($F_{9,61} = 4.7$, $p = 0.0054$ and $F_{9,61} = 37.9$, $p < 0.0001$, respectively). Importantly however, there was a site \times time interaction for both abundance ($F_{9,61} = 11.2$, $p < 0.0001$) and taxa ($F_{9,61} = 2.5$, $p = 0.0176$). This was influenced by site-specific variation in the relative dominance of taxa in the ambient community (Appendix 1) as well as species-specific seasonality in recruitment patterns (see next section).

Ambient community and rates of bedload dispersal

The number of taxa and abundance in the ambient community was variable in time and space. For the

total number of taxa, there was a significant effect of site (fixed factor 2-way ANOVA; $F_{3,224} = 17.0$, $p < 0.0001$) and time ($F_{3,224} = 16.6$, $p < 0.0001$). Also for abundance there was a significant effect of both site ($F_{3,224} = 15.0$, $p < 0.0001$) and time ($F_{3,224} = 15.9$, $p < 0.0001$). Similarly to the dispersing community, there was also a significant site \times time interaction for both taxa ($F_{18,224} = 2.3$, $p < 0.0032$) and abundance ($F_{18,224} = 8.0$, $p < 0.0001$), illustrating that patterns of variability were not consistent. Much of this variability was related to species-specific variability in responses across sites and times. In the ambient community, the bivalve *Macoma balthica*, Ostracoda and Oligochaeta were the most dominant taxa (Fig. 4 and Appendix 1), each one respectively accounting for $>20\%$ of total ind. (together = 70.4%). Despite their high abundance in the ambient community, Oligochaeta and *M. balthica* only accounted for 2.5 and 2.8%, respectively, of

dispersing individuals. Relative dispersal rates also reflected this trend, with both Oligochaeta and *M. balthica* having substantially lower rates than Ostracoda. Within the ambient community, *M. balthica* was most abundant at the most sheltered site, where it also

showed the highest heterogeneity over time (Appendix 1). In the ambient community, Oligochaeta abundance increased in a 1:1.2:1.9:3 ratio towards the more exposed site, but Oligochaeta dispersal rates were not in proportion to site-specific differences in

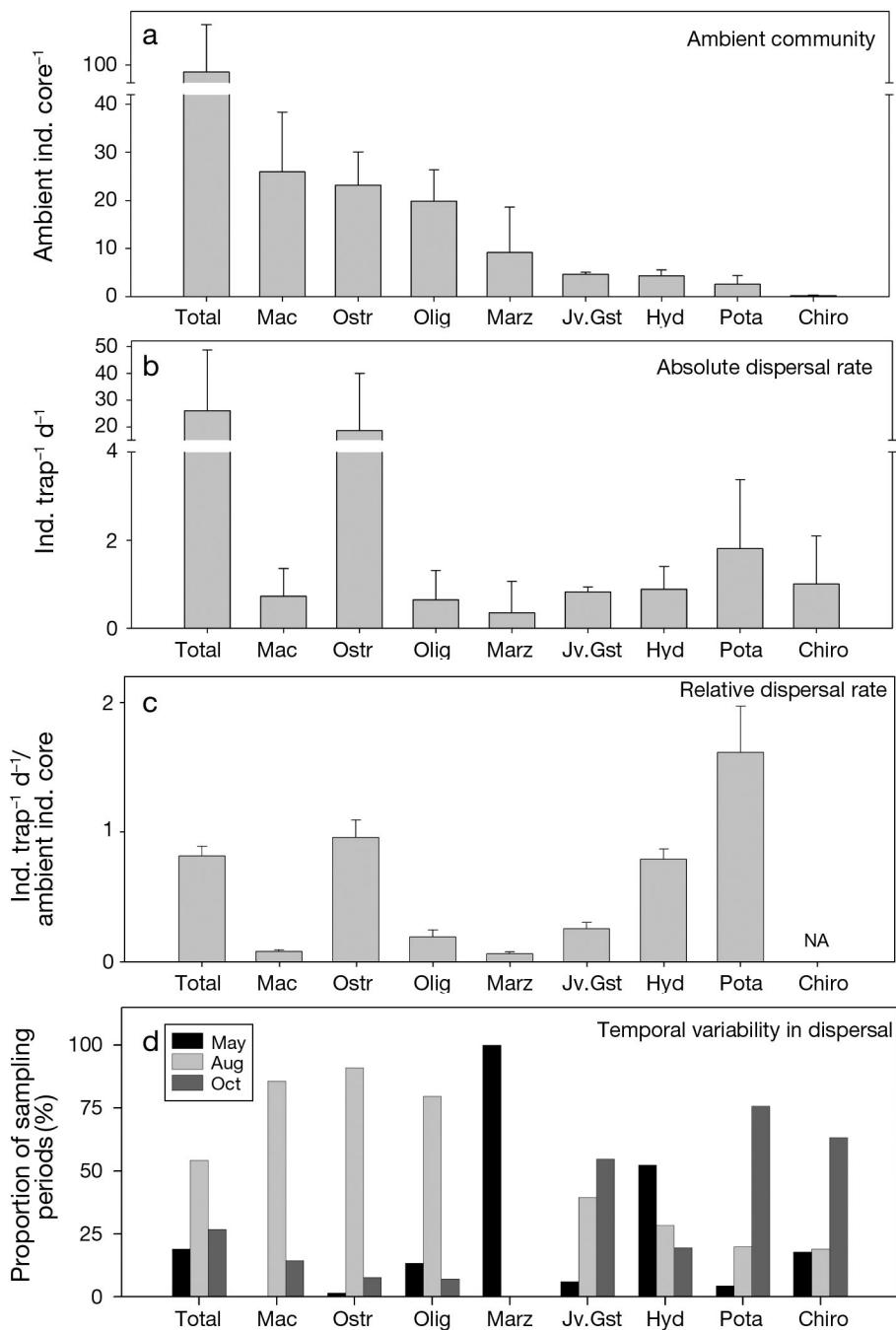


Fig. 4. (a) Ambient community densities, (b) absolute and (c) relative dispersal rates, and (d) temporal variability in dispersal for the most abundant taxa (91.5 % of ambient and 95.3 % of dispersing individuals) at all 4 sites and times (mean \pm SE). Note vertical axis breaks in 2 of the graphs. Total = all species total number of individuals; Mac = *Macoma balthica*; Ostra = Ostracoda; Oligo = Oligochaeta; Marz = *Marenzelleria* sp.; Hyd = *Hydrobia ulvae*; Pota = *Potamopyrgus antipodarum*; Jv.Gst. = Juvenile gastropod; Chiro = Chironomidae; NA = undefined due to 0 value in denominator of rate calculation

ambient community abundances. Ostracoda were the most abundantly caught taxa in traps, accounting for 71 % on average of total number of dispersing individuals (Fig. 4). This can partly be attributed to their high abundance in the ambient community, epifaunal position and semi-mobile living habit. Absolute dispersal rates of Ostracoda were higher towards more exposed sites, with rates increasing in a 1:3.5:14.3:25 ratio from sheltered to exposed, where they also exhibited a larger heterogeneity in abundance over time (Appendix 1). Adults as well as juveniles of the gastropods *Potamopyrgus antipodarum* and *Hydrobia ulvae*, were recorded regularly both in traps and in the ambient community (Appendix 1), which was also indicated by their relatively low VMR in comparison to other species that exhibited high stochasticity in rates of bedload dispersal over time. For these 2 very similar gastropod species, *H. ulvae* had a higher average ambient abundance (4.1 ind. core⁻¹) and a lower (0.9 ind. d⁻¹) but steady dispersal rate (VMR: 1.2), whereas *P. antipodarum* had a lower ambient abundance (2.6 ind. core⁻¹), but higher (1.9 ind. d⁻¹) and more variable dispersal rate (VMR: 3.3). Despite both species being relatively abundant in the ambient community in autumn, *P. antipodarum* was found to have higher rates of dispersal during this period (Fig. 4). When considering juvenile gastropods (<1 mm shell length), their proportion of all gastropods in the ambient community was 28 % in May, 56 % in July and 29 % in the October sampling in 2007. When considered separately, juvenile gastropods had the highest dispersal rates in October. In early summer (May), *Marenzelleria* sp. was found to be more abundant in the ambient community with higher dispersal rate, than average across all times (Fig. 4). This early seasonal peak in abundance and the fact that *Marenzelleria* sp.'s time averaged ambient abundance and dispersal rates were comparable to that of other species, would suggest a life-history with a comparatively more pronounced peak in recruitment. In addition, *Marenzelleria* sp. also had both greater ambient abundance and rates of dispersal towards more sheltered sites (Appendix 1). Chironomids were found to be virtually absent from the ambient community, but showed quite high dispersal rates, especially towards later summer month sampling occasions. Dispersal rates were also higher towards the more exposed sites. Total dispersal was highest in July (54 %), which was twice as high as in May (19 %) or October (27 %). Proportionally, the most dispersal occurred when post-larval recruits are expected to be present in high numbers available for bedload transport. *M. balthica*, Ostracoda and Oligochaeta followed a similar trend, all having relatively higher dispersal rates during late summer (July sampling), than later on in autumn (October) or early in summer (May; Fig. 4).

When comparing VMR over time, the number of dispersing taxa showed higher heterogeneity (86.4) than the ambient community (9.9).

Site-specific environmental conditions and dispersal

Granulometry and hydrodynamics

Median grain size (d_{50}), estimated friction velocity (u_*) and percentage of sediment that was cohesive (i.e. <0.063 mm) indicate a clear gradient across sites (A–D) of sheltered to exposed (Table 1). Exposure based on a GIS-based model (Isaeus 2004) indicated that Sites C and D were similar in exposure and were on average more exposed than Sites A and B, which were again similar in exposure. Higher exposure to waves at Site C and D would imply a more stochastic energy supply regime, in contrast to the wave-sheltered Sites A and B. These predictions were reflected in the granulometry of the sites, with higher scatter (S_1) in grain size distribution indicative of poorly sorted sediment at the more exposed Sites C and D, in comparison to the relatively well sorted sediment of Sites A and B (Table 1).

Site A had the most well-sorted and finest grain size distribution, with the highest fraction of cohesive sediment and the relatively highest differences between estimated and predicted friction velocity (Table 1). Site B, despite being quite sheltered from waves, had relatively high estimated friction velocity (u_*) with quite well-sorted sediment, which was in agreement with observed relatively strong episodic currents at the site (authors' pers. obs.). Site C was closest to its sediment erosion threshold, with the smallest difference between estimated and predicted friction velocity (Table 1). Site C also had the least sorted sediment, indicative of a stochastic energy regime. It had a grain size that was finer than expected from the site's relative exposure. The largest accumulations of drift algal material were also observed at Site C (authors' pers. obs.). The most exposed Site D had the coarsest sediment (d_{50}) and highest estimated friction velocity of all sites.

Dispersal in relation to sediment and algal transport

Average rates of sediment transport were highest at Site B (mean: 1.16 g sediment d⁻¹), then Site D (0.48 g d⁻¹), followed by C (0.40 g d⁻¹), then A (0.22 g d⁻¹) (Fig. 5f). At Sites B and D, rates of relative dispersal were the most related to sediment transport, as indicated by the increase in relative rates of dispersal in the upper quantiles (0.90 and 0.99) as sediment transport increased. In turn, average algal transport was

highest at Site C (mean: $0.151 \text{ g algae d}^{-1}$), followed by Site D (0.110 g d^{-1}), Site B (0.034 g d^{-1}) and Site A (0.013 g d^{-1}) (Fig. 6f). At sites that had more algal transport (Site C and D), a clear difference in relative dispersal rates was observed in the upper quantiles (0.90 and 0.99) as rates of algal transport increased.

When comparing mean relative dispersal rate (ind. trap $^{-1}$ d $^{-1}$) between sites, it was highest at Site C

(0.50), followed by Sites D (0.47), B (0.18) and A (0.07) (Table 1). Across all sites, mean rates of dispersal (0.50 quantile) were neither directly dependent on amounts of sediment nor on algal transport, but when considering the 0.90 and 0.99 quantiles in mean, a site-dependent response was observed when amounts of sediment and algal transport increased (Figs. 5 & 6, respectively). A threshold in dispersal

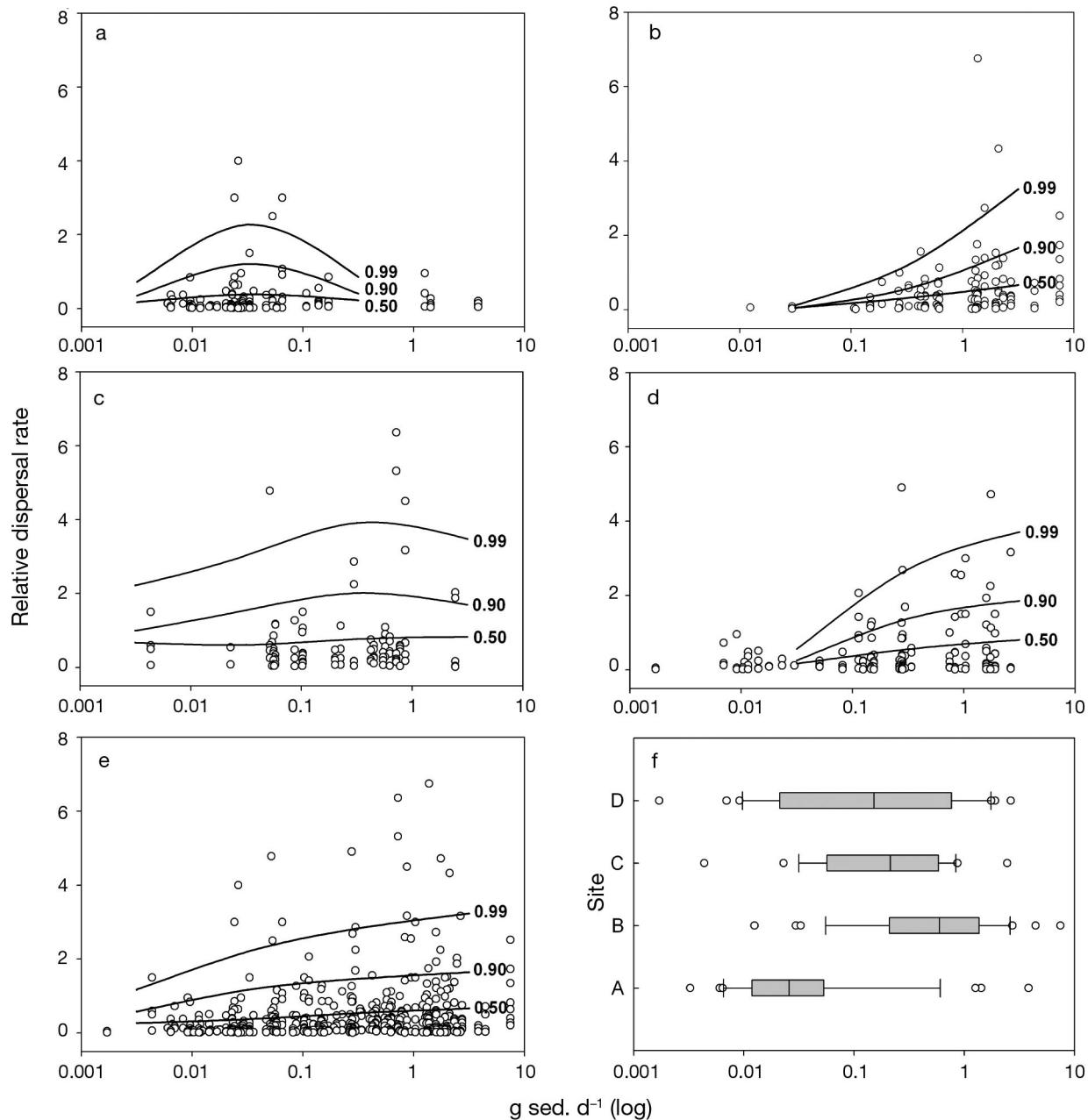


Fig. 5. Relative dispersal rates of species caught in traps with increasing sediment transport on a log scale separately for Sites (a) A, (b) B, (c) C, (d) D, and (e) at all sites. Lines: changes in mean (0.50) and upper quantile relative dispersal rates (0.90 and 0.99) across different rates of sediment transport. (f) Site-specific mean amounts of sediment transport

rates at Sites B and D was also apparent when comparing VMR in the number of species in traps at each site (Table 1). Sites B and C had a quite heterogeneous distribution (i.e. larger difference in the number of taxa dispersing), with a VMR of 1.64 and 2.03, respectively. Sites A and C had a more homogenous distribution (i.e. either steadily low or steadily high number of species dispersing) with VMRs of 1.01 and

0.86 in the number of species in traps, respectively. When comparing ratios of absolute dispersal in traps with $>0.1 \text{ g sediment d}^{-1}$ to those with $<0.1 \text{ g sediment d}^{-1}$, Sites B and D also exhibited dispersal that was more associated with sediment transport (Table 1). Similarly the ratio of number of species associated with traps with higher rates of sediment transport compared to those with lower rates was

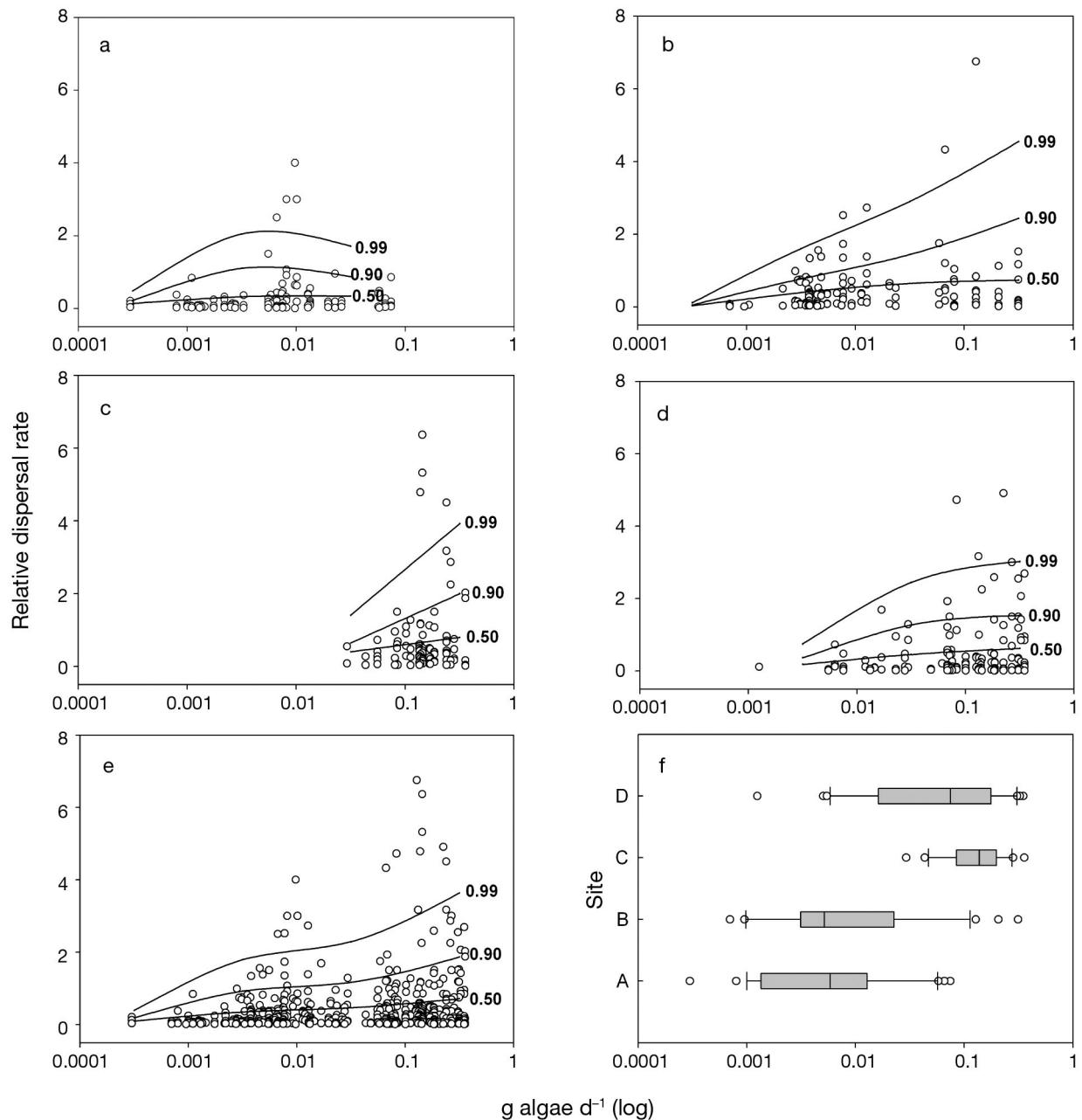


Fig. 6. Relative dispersal rates of species caught in traps with increasing algal transport on a log scale for Sites (a) A, (b) B, (c) C, (d) D, and (e) at all sites. Lines: changes in mean (0.50) and upper quantile relative dispersal rates (0.90 and 0.99) across different rates of algal transport. (f) Site-specific average amounts of algal transport

higher at Sites B and D than at C and A. When considering the ratio of individuals and species associated with larger amounts of algal transport ($>0.01 \text{ g algae d}^{-1}$) compared to small amounts ($<0.01 \text{ g algae d}^{-1}$), dispersal at Site D was more associated with algae than at Sites A and B (Table 1).

Size-dependent dispersal

Macoma balthica

With increased rates of sediment transport, both the size and number of dispersing *Macoma balthica*

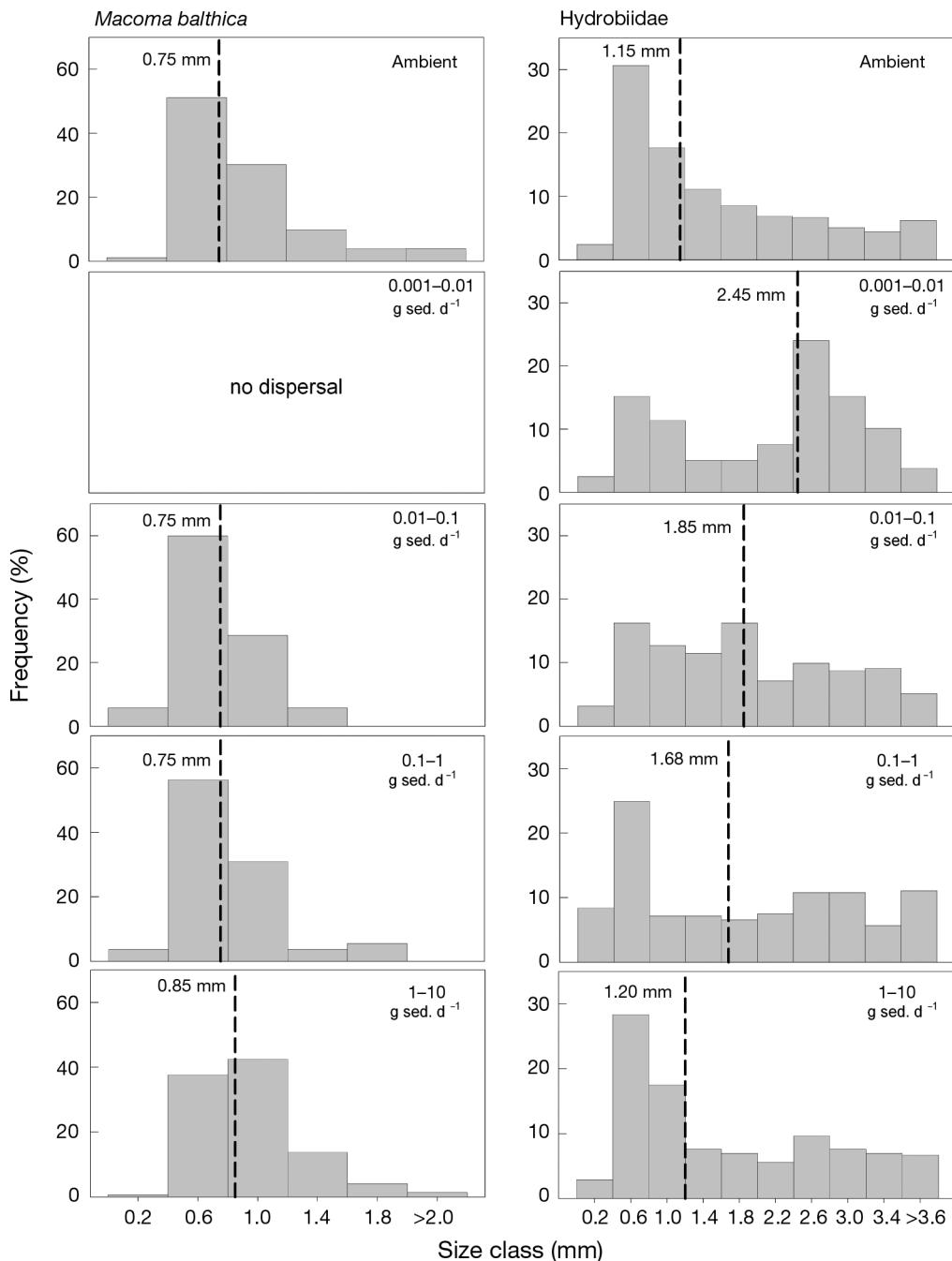


Fig. 7. Size frequency distribution (%) and median size (dashed line) of the bivalve *Macoma balthica* and the gastropod Hydrobiidae in ambient cores and in 4 different classes of increasing rates of sediment transport (g sediment d^{-1}) on a log scale

Table 2. (A) Statistical analysis using a Mann-Whitney (M-W) and Kolmogorov-Smirnov (K-S) test on differences in median sizes and size frequency distribution of *Macoma balthica* and Hydrobiidae in ambient community in relation to different rates of sediment transport (g sediment d⁻¹) on a log scale. (B) Sizes: mean and median of individuals. n (repl⁻¹): number of ind. core⁻¹ or trap⁻¹; n: total number of ind. in all respective cores or traps. NS: not significant; -: not found in sediment class

		A. Statistical analysis				
		Ambient	0.001–0.01	0.01–0.1	0.1–1	1–10
Macoma balthica	M-W test				K-S test	
Ambient			–	–	0.202	NS
0.001–0.01		–	–	–	–	–
0.01–0.1	115489	NS	–	–	0.086	NS
0.1–1	175143.5	NS	–	–	965	NS
1–10	359854	p<0.001	–	–	3372.5	p<0.001
Hydrobiidae	M-W test				K-S test	
Ambient			0.314	p<0.001	0.221	p<0.001
0.001–0.01	70729	p<0.001	–	–	0.178	p=0.044
0.01–0.1	267232.5	p<0.001	9422.5	NS	–	–
0.1–1	396171	p<0.001	10819	p=0.013	40480.5	NS
1–10	422271.5	p=0.014	10136	p<0.001	37847.5	p<0.001

B. Sizes					Hydrobiidae
	Mean	Median	n (repl. ⁻¹)	n	
Macoma balthica					
Ambient	0.87	0.75	24.7	6235	
0.001–0.01	–	–	0	0	
0.01–0.1	0.72	0.75	0.9	35	
0.1–1	0.77	0.75	1.2	55	
1–10	0.94	0.85	6.1	146	
Hydrobiidae					
Ambient	1.51	1.15	10.7	2688	
0.001–0.01	2.15	2.45	6.6	79	
0.01–0.1	1.98	1.85	6.5	266	
0.1–1	1.84	1.68	7.3	334	
1–10	1.67	1.20	14.3	342	

increased (Fig. 7, Table 2). In the ambient community, within the size range of individuals caught in traps (0.0–3.4 mm), *M. balthica* had a median size of 0.75 mm, with 17.5 % of individuals >1.2 mm. At lowest rates of sediment transport (0.001–0.01 g sediment d⁻¹), no *M. balthica* were recorded in traps. At 0.01–1 g sediment d⁻¹ the number of dispersing individuals (trap⁻¹) was quite low, but once rates of sediment transport increased (>1 g d⁻¹) absolute rates of dispersal increased. At these high rates of sediment transport, the median size of *M. balthica* (0.85 mm) was significantly larger than at lower rates (Table 2), illustrating that larger bivalves have a higher erosion threshold. Similarly, the size distribution was significantly different at lower rates of sediment transport (Table 2). In the ambient community and at low rates of sediment transport, the proportion of individuals between 0–0.8 mm was >50 %. The proportion of individuals in this size-class decreased to 38 % as rates of sediment transport increased (Fig. 7).

With increased rates of sediment transport, size of Hydrobiidae decreased and the total number of dispersing Hydrobiidae increased (Fig. 7, Table 2). Once rates of sediment transport increased (>1 g sediment d⁻¹), absolute rates of dispersal (ind. trap⁻¹) increased 2-fold (Table 2). Ambient community Hydrobiidae had a median size of 1.15 mm, with 51 % of individuals <1.2 mm. When sediment transport was highest (>1 g d⁻¹), median Hydrobiidae were 1.20 mm, with 49 % of individuals <1.2 mm. Hydrobiidae in the ambient community and at high sediment transport rates had significantly different size-frequency distributions as well as median size. Larger differences were noted at lower rates of sediment transport where the median size of Hydrobiidae increased significantly to 1.68, 1.85 and 2.24 mm in consecutively smaller classes of sediment transport (Table 2). Similarly, the proportion of individuals <1.2 mm decreased to 40, 32 and 29 % of individuals. The largest individuals were recorded at the lowest rates of sediment transport (<0.01 g d⁻¹).

DISCUSSION

In general we found that dispersal patterns across our sites over time did not reflect any single factor acting alone. Rates of bedload dispersal depended on taxa- and site-specific characteristics, temporal and seasonal variability, as well as amounts of drift-algal and sediment transport. Our study sites did, however, show a gradient from sheltered to exposed (A–D) in terms of median grain size and estimated friction

velocity. In agreement with our previous study (Valanko et al. 2010), we found that the dispersing community exhibits higher heterogeneity than the ambient community in terms of number of both taxa and individuals. This could suggest that even with high variability in sediment transport and dispersing fauna, resident ambient communities are quite persistent (see also Hewitt et al. 1997, Norkko et al. 2001). Site-specific differences were observed when considering variation in the mean dispersal rates (0.90 and 0.99 quantiles). Dispersal was found to be the sum of several interacting factors (Fig. 1), where differences across sites in dispersal rates can partly be explained by species-specific dispersal rates and modes differentially modified by environmental constraints, similar to findings of Turner et al. (1997) on a tidal sandflat in New Zealand.

Species-specific dispersal rates

Of the 3 most abundant taxa in the ambient community (*Macoma balthica*, Oligochaeta and Ostracoda), only Ostracoda showed consistently high abundances in the dispersing community as well, across both sites and times. These results are consistent with those of Committo & Tita (2002) who also found that Ostracoda and Oligochaeta had very high and very low dispersal rates, respectively. Higher dispersal rates in the bedload and rates that were in proportion to exposure at sites (i.e. higher dispersal at sites with more energy) can be attributed to taxon-specific characteristics. Ostracoda have an epifaunal position and are relatively passive in their dispersal mode (Valanko et al. 2010). Similarly, Chironomidae also exhibited dispersal rates that were in proportion to site exposure and they were also associated with higher rates of algal transport. Oligochaetes in the ambient community were more abundant towards more exposed sites, but in contrast, were not found to disperse in a similar proportion across sites, suggesting active dispersal, although at low rates. Similarly, on a north-eastern US mudflat, Junkins et al. (2006) found no correlation between rates of Oligochaete emigration or immigration and their local density in the sediment. They also suggest that Oligochaeta are able to both actively emerge from the sediment into the water column, and leave the water column and return to the sediment, as also found by Nilsson et al. (2000).

In general, *Macoma balthica* had low relative dispersal rates across all sites. In contrast, at high-energy tidal locations (max. current speed: 90 cm s⁻¹), a similar bivalve, *Mya arenaria*, has been reported as having daily transport rates exceeding their ambient density (Hunt et al. 2007). In the ambient community, *M. balth-*

ica was found to be most abundant with the largest variability over time at the most sheltered site, which indicates higher rates of recruitment and a preference for sheltered finer sediment sites. St-Onge & Miron (2007) showed that juvenile *M. arenaria* clams were eroded in greatest numbers in sand while mud retained them more easily. Beukema (1993) has shown that upon initial recruitment (0.1–1 mm), *M. balthica* show a preference to shallow sheltered sites, with fewer disturbances and where growth is more rapid. He suggests that as adults, they move to deeper waters in response to more favorable conditions that support higher survival, growth rates and reproductive output. However, Beukema's study was conducted in a tidal system where the potential for active migration is greater; our findings suggest that dispersal of larger *M. balthica* is associated with higher rates of sediment transport. As an infaunal species, larger *M. balthica* individuals are able to burrow deeper and resist erosion, while shallower living smaller individuals are more susceptible to erosion. Our findings indicate that at high rates of sediment transport, the proportion of bivalves <1.2 mm in the dispersing community (80.8%) was similar to that of the ambient community. At lower rates of sediment transport, the proportion of dispersing bivalves <1.2 mm increased to 94.3%, which indicates resistance to erosion by larger individuals. Similarly, Norkko et al. (2001) found higher erosion rates for juvenile bivalves <1 mm than those sized between 1 and 4 mm on a New Zealand sandflat, illustrating the strong size-dependence in dispersal potential. Nevertheless, while there generally is a tendency for smaller sized individuals to exhibit higher rates of dispersal, Committo et al. (1995b) found the opposite pattern in the brooding bivalve *Gemma gemma*.

Juvenile gastropods, *Potamopyrgus antipodarum* and *Hydrobia ulvae* all exhibited quite a steady occurrence in both traps and ambient community across sites and times, indicated by their relatively low VMR and high relative dispersal rates in comparison to other species. In terms of surface area, Hydrobiidae have a larger realized spatial niche than that of more sedentary infaunal species. The invasive gastropod *P. antipodarum* was relatively more abundant in late summer (July sampling) while the native *H. ulvae* was more abundant in early summer (May sampling), indicating a degree of seasonal niche differentiation between these 2 very similar species. *P. antipodarum* had lower overall ambient abundance but higher and more variable dispersal rates, indicating higher colonization ability, which is characteristic of invasive species. When considering Hydrobiidae as a group, differences in size-frequency distribution were observed with increasing sediment transport: larger Hydrobids were associated with lower rates of sediment transport. With

increasing sediment bedload transport, the size frequency distribution shifted to that of the ambient community. Günther (1992) suggests that *H. ulvae* disperse less frequently once they exceed 1 mm length. Our results indicate that small gastropods are more dependent on sediment bedload transport while larger individuals are able to exhibit more active epifaunal living behavior.

Temporal variability

While total abundance and number of taxa of the dispersing community indicated large variation in both time and across site, the ambient community was in comparison quite stable. With quiescent wind conditions in May 2007, when mean 2-day conditions were 1.2 m s^{-1} lower than the monthly mean, abundance and number of taxa dispersing was low with small differences between sites. In contrast, during higher wind conditions in July and August 2006, when mean 2-day conditions were 2.6 and 4.5 m s^{-1} higher than the monthly mean, respectively, highest abundance and number of taxa dispersing were recorded with a large difference between sites. Similarly, when considering VMR of relative dispersal rates (ind. d^{-1}) for each site across all times, they showed a steady increase towards the more exposed sites (Table 1). This would suggest that post-larval bedload dispersers are more sensitive to changes in abiotic conditions towards more exposed sites. Our results showed little change in terms of number of individuals and number of taxa in the ambient community across sampling times. This lack of strong temporal variability in the ambient community indicates that post-larval dispersal does play a role in maintaining population dynamics. In 2007, highest dispersal rates were recorded in the July sampling, which coincided with the presence of post-larval recruits and thus their availability for bedload transport. In contrast, the lowest number of dispersing species was recorded when sampling in May; although this time also coincided with 2-day mean wind conditions that were lower than the monthly mean. During this period, *Marenzelleria* sp. showed higher ambient abundance and dispersal rates, suggesting a life-history with a pronounced seasonal peak in recruitment.

Site-specific patterns in dispersal

Our field study was designed to look for generality in bedload dispersal rates across time and space in a multi-species context. In contrast to laboratory flume conditions, the nature of our observational field study demonstrates a very heterogeneous response distribu-

tion. This is typical for field experiments, as they often incorporate interactions among measured and unmeasured ecological factors, all contributing to the pattern of interest (e.g. Cade & Noon 2003). In our case, rates of bedload dispersal were potentially influenced by site-specific environmental differences, an interaction between amounts of sediment and algae, time of sampling, along with species-specific behavior (Fig. 1). More specifically, we wanted to address how between-site differences in relative dispersal rates changed with increasing sediment and algal material transport.

Compared to the other sites, Site A had low rates of sediment and algal transport, and fine-grained and more cohesive sediment. Overall, relative dispersal rates were much lower than average across all sites. Gastropod snails are epifaunal and able to actively move and, therefore, relatively less dependent on passive bedload transport. As expected *P. antipodarum* had the highest relative dispersal rates of species at the most sheltered Site A. In comparison, species that can be considered more passive in their dispersal mode, such as Ostracoda, Oligochaeta, juvenile gastropods, and Chironomidae, showed higher dispersal rates towards the more exposed Site D, with the coarsest sediment and highest estimated friction velocity. Ostracoda, for example, exhibited relative dispersal rates across sites that were directly in proportion to the site's exposure.

When considering exposure to waves and sorting of sediments, Sites C and D were more exposed with mixed sediment grain sizes indicative of a more variable energy regime (i.e. higher frequency of wind-wave events). Site C had the least sorted grain size distribution as well as the finest grain size relative to its exposure to waves. This was also reflected in Site C being closest to its critical friction velocity (Table 1), suggesting relatively higher re-suspension and deposition rates. Despite high relative dispersal rates, Site C did not show a clear threshold in upper quantile (0.90 and 0.99) rates of relative dispersal with increasing amounts of sediment transport (Fig. 5). At these more exposed sites, relatively larger amounts of algae were also recorded. Drift algae can be an important transport vector for post-larvae in the bedload, as it has been found to harbour very high abundances (up to $1116 \text{ ind. g dry wt algae}^{-1}$) of associated fauna (Norkko et al. 2000). Similarly, at Site C, the highest mean relative dispersal rate was recorded together with consistently high rates of algal transport at all times (all traps $>0.01 \text{ g algae d}^{-1}$; Fig. 6).

Site B was relatively sheltered to waves, with well-sorted sediment in combination with relatively high estimated friction velocity, indicative of a steady energy regime (probably currents; authors' pers. obs.). Site B had the highest rates of sediment transport, and

the relative dispersal rates were more closely associated with higher rates of sediment bedload transport. Similarly, at Site D, higher species relative dispersal rates exhibited an association to larger amounts of sediment transport. Sites B and D showed the clearest thresholds in dispersal, with their response in the upper quantiles (0.90 and 0.99) with increasing amounts of sediment transport. In addition to this pronounced threshold in dispersal potential, there was also an overall large variation in the number of species dispersing. Once a site's sediment erosion threshold is exceeded, species erosion occurs and subsequent dispersal will take place (Armonies 1994; Fig. 1). Similarly, in tidal areas, it has been shown that rates of bedload dispersal are associated with sediment re-suspension and exposure (e.g. Lundquist et al. 2006). In tidal systems, stochastic wind-wave events have been found to be very important and contribute to strong site-specific differences in bedload transport and the erosion and dispersal of fauna (Norkko et al. 2002). In our non-tidal system, such stochastic events are likely to play a major role, although it does not preclude continuous dispersal from taking place even in more moderate conditions, as indicated by our study. Nevertheless, in comparison to systems with more hydrodynamic forcing, our overall rates of bedload transport and dispersal are reasonably low (this study, Valanko et al. 2010).

Our study incorporated several measures of bedload dispersal in parallel, which Commito & Tita (2002) suggest is necessary to avoid pitfalls in interpreting results from single measures of dispersal. Caution should also be taken when directly comparing ambient community density (X) with dispersing number of individuals (Y), as sampling methods are often not comparable. Methods used may sample completely different aspects of dispersal (i.e. depending on the question being addressed) and have varying volumes and surface areas compared to ambient community sampling (see Valanko et al. 2010). We propose that species-specific proportional size-frequency distributions, in respective sampling methods, could be used to investigate whether a species is dispersing in proportion to its ambient community. In addition, measures of heterogeneity in distribution (e.g. VMR) across space and time can give an indication of how well dispersal patterns mirror the ambient community composition, as they are not as dependent on abundance alone. Future studies should thus concentrate on specific mechanisms of dispersal. For example, to better understand the underlying mechanisms affecting species-specific dispersal rates in non-tidal systems, species-specific susceptibility to erosion with short-term changes in hydrodynamic conditions should be investigated. When interpreting dispersal patterns and making com-

parisons between species, it is also important to be cognizant that the temporal scales involved can range from seconds to seasons, and the spatial scales from cm to km (Armonies 1994). This is difficult to encompass in the same study. Nevertheless, to better understand connectivity in a meta-community context, the temporal scale of findings needs to bridge between studies done from direct measurements of dispersal with studies done looking at spatial connectivity by linking species richness at different scales (e.g. Cadotte 2006, Thrush et al. 2008, 2009).

In conclusion, our findings demonstrate that post-larval bedload dispersal is an important process in non-tidal systems, and is temporally variable and dependent on an interaction between species-specific characteristics, site-specific hydrographic conditions at the time of observation and grain size characteristics (Fig. 1). Further studies are also needed to shed light on both the limitations and potential of different dispersal mechanisms for benthic communities, as they are the drivers of the potential thresholds in benthic recovery processes (Norkko et al. 2010). Within a non-tidal system such as the Baltic Sea, an understanding of the connectivity between benthic communities and how they may persist in the face of increased habitat fragmentation, with increasing spatial and temporal scales of disturbance, is essential (i.e. hypoxia, Norkko & Bonsdorff 1996, Conley et al. 2009). Importantly, while patterns of post-larval dispersal may be highly variable in both time and space, it clearly plays a central role in the population and patch dynamics of many benthic invertebrates. While the distribution of species is heavily influenced by the peaked larval recruitment period over large spatial scales, the net result of continuous small-scale dispersal events is clearly also very important in maintaining populations. It is interesting to hypothesize whether the contribution of later stage post-settlement dispersers may in fact be as important or even more so than the initial larval recruits to the mature adult population due to the relatively higher survival rates and extended period of dispersal of the post-settlers.

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Appendix 1. Total and species-specific ambient community abundances (ind. core⁻¹) and absolute dispersal rates (ind. trap⁻¹ d⁻¹) presented separately for each site (A–D) and time (mean ± SE). The 8 most abundantly occurring taxa (91.5 % of ambient and 95.3 % of dispersing ind.) are shown. Date: deployment date of traps (retrieved after 48 h) and sampling of ambient cores. Including: *Macoma balthica*; *Hydrobia ulvae*; *Potamopyrgus antipodarum*; Juvenile (Juv.) gastropod Ambient community (ind. core⁻¹)

Year date	Site	n	Total		<i>M. balthica</i>		Ostracoda		Oligo- chaeta		<i>Marenzel- leria</i> sp.		Juv. gastropod		<i>H. ulvae</i>		<i>P. antipo- darum</i>		Chiro- nomidae	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ambient community (ind. core⁻¹)																				
2006																				
31 Jul	A	3	136.1	31.4	105.8	23.6	7.3	2.5	11.8	4.3	2.2	0.6	0.3	0.0	3.7	1.3	0.1	0.1	–	–
	B	3	91.7	2.9	55.8	3.8	11.2	2.7	14.7	5.0	3.1	0.2	0.8	0.5	1.8	0.1	0.2	0.2	–	–
	C	3	79.7	7.2	14.8	0.3	27.1	5.2	16.4	2.4	8.0	1.0	0.2	0.2	3.4	0.5	0.1	0.1	1.2	1.2
	D	3	134.9	20.7	17.0	0.7	67.4	17.9	39.3	5.8	2.1	0.7	0.2	0.1	1.3	0.7	0.2	0.1	0.1	0.1
12 Aug	A	3	116.2	6.8	76.9	4.6	10.6	1.0	8.6	3.3	4.0	1.2	2.3	0.8	2.4	0.6	0.6	0.3	–	–
	B	3	124.1	6.9	58.8	7.2	16.0	2.0	32.6	4.7	3.2	0.7	2.6	0.8	2.2	0.4	0.1	0.1	–	–
	C	3	107.7	11.2	28.3	4.0	26.6	7.4	32.1	3.8	5.6	1.1	1.7	0.5	1.7	0.4	0.1	0.1	–	–
	D	3	119.2	15.0	17.6	3.6	29.9	3.5	50.2	8.1	2.1	0.9	3.6	1.3	1.4	0.2	0.2	0.2	–	–
29 Aug	A	3	121.7	7.0	69.0	7.1	16.0	0.7	13.7	1.0	3.6	0.4	4.8	1.3	2.3	0.7	1.0	0.7	–	–
	B	3	63.8	5.5	20.3	2.4	16.7	2.7	8.8	2.1	1.8	0.3	4.9	0.1	3.9	0.9	2.9	0.6	–	–
	C	3	87.0	14.6	12.1	1.6	24.4	2.3	35.0	15.2	3.8	0.3	1.3	0.2	3.0	0.7	0.7	0.2	0.2	0.1
	D	3	83.2	7.7	14.4	0.9	15.2	3.3	27.9	2.8	1.7	0.6	6.9	1.1	5.9	1.0	2.3	0.8	0.2	0.1
17 Oct	A	3	97.4	8.6	28.6	2.8	14.9	3.3	24.0	4.1	2.9	0.6	7.2	3.6	8.1	1.5	0.6	0.1	0.7	0.0
	B	3	70.9	12.5	12.3	2.8	20.8	4.2	11.7	4.5	1.4	0.2	6.4	0.9	6.0	1.0	5.8	1.1	0.6	0.4
	C	3	49.6	5.8	7.0	0.5	14.2	1.9	14.1	3.6	2.9	0.7	1.7	0.5	2.0	0.5	1.8	0.6	0.1	0.1
	D	3	122.1	7.7	8.8	1.6	28.6	3.6	49.1	4.6	1.0	0.5	5.4	0.2	6.2	2.5	6.2	0.6	0.6	0.6

Appendix 1 (continued)

Year date	Site	n	Total		<i>M.</i> <i>balthica</i>		Ostracoda		Oligo- chaeta		<i>Marenzel-</i> <i>leria</i> sp.		Juv. gastropod		<i>H.</i> <i>ulvae</i>		<i>P. antipo-</i> <i>darum</i>		Chiro- nomidae		
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Ambient community (ind. core⁻¹) (continued)																					
2007																					
09 May	A	3	145.2	10.8	23.1	3.6	11.9	2.4	7.0	1.2	90.3	13.6	1.2	0.3	4.7	0.7	0.3	0.3	0.2	0.1	
	B	3	110.7	15.0	9.7	1.2	6.6	2.1	14.6	2.5	63.4	8.7	3.6	1.7	3.1	0.5	3.0	0.7	0.4	0.2	
	C	3	68.3	13.4	6.0	0.5	20.7	6.9	16.2	8.4	13.8	3.6	1.3	0.7	3.7	0.5	1.0	0.5	—	—	
	D	3	60.9	18.0	6.6	2.4	8.1	2.1	24.3	6.4	4.1	0.8	2.2	0.4	6.8	2.7	2.6	0.8	0.1	0.1	
25 Jul	A	3	112.1	15.5	40.4	7.8	34.9	4.0	7.3	1.3	9.6	1.4	5.6	0.9	4.1	0.8	0.9	0.6	—	—	
	B	3	71.9	15.0	15.7	2.2	32.8	8.3	4.9	2.3	2.9	0.7	5.6	2.2	1.3	0.5	1.3	0.5	—	—	
	C	3	74.1	10.4	10.1	1.7	29.0	7.7	12.9	3.3	8.3	0.6	3.0	0.7	2.3	0.8	1.3	0.5	—	—	
	D	3	123.3	5.1	18.3	3.0	30.3	1.9	47.0	5.3	3.3	0.7	7.9	1.7	4.1	1.4	1.6	0.6	—	—	
09 Oct	A	3	64.0	4.7	9.2	2.1	20.9	3.1	10.2	3.4	2.2	0.7	1.3	0.4	7.4	1.6	1.3	0.6	0.3	0.0	
	B	3	113.7	10.3	6.8	1.0	53.7	5.4	8.7	0.3	2.0	0.2	17.6	4.2	11.4	0.8	6.4	1.6	0.2	0.1	
	C	3	106.6	11.6	8.9	0.4	30.8	0.2	27.2	11.1	5.0	0.7	8.4	1.2	2.0	0.2	12.6	2.3	0.3	0.2	
	D	3	110.4	11.5	9.2	0.4	35.0	8.8	12.8	4.7	1.8	0.6	18.3	3.3	8.3	1.4	16.8	1.1	—	—	
Absolute dispersal (ind. trap⁻¹ d⁻¹)																					
2006																					
31 Jul	A	5	8.4	1.2	3.5	0.8	2.2	0.5	0.4	0.2	—	—	—	—	1.2	0.6	0.3	0.2	—	—	
	B	4	12.3	2.9	1.8	0.5	8.0	2.6	0.8	0.1	—	—	—	—	0.8	0.4	0.1	0.1	0.1	0.1	
	C	2	100.8	87.8	—	—	90.0	82.5	2.0	1.0	—	—	—	—	1.5	1.0	0.3	0.3	3.5	3.0	
	D	5	179.8	53.0	0.5	0.3	168.1	49.4	1.2	0.2	—	—	—	—	1.4	0.5	0.1	0.1	6.4	3.1	
12 Aug	A	5	8.0	0.9	2.9	0.7	2.3	0.7	0.3	0.1	—	—	0.5	0.4	0.7	0.4	1.0	0.3	—	—	
	B	4	25.3	6.3	3.5	0.7	17.9	4.9	0.3	0.2	—	—	1.8	0.6	0.1	0.1	1.0	0.5	0.2	0.1	
	C	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
	D	4	104.6	18.7	0.8	0.4	91.5	18.8	0.3	0.1	0.1	0.1	2.7	0.3	0.7	0.2	0.3	0.1	2.8	0.7	
29 Aug	A	5	13.0	3.3	0.6	0.3	2.3	1.0	3.5	2.3	—	—	1.1	0.6	1.4	0.4	2.8	0.4	0.3	0.1	
	B	5	47.6	6.3	3.0	0.7	28.9	6.3	1.3	0.6	—	—	1.9	0.8	1.5	0.4	8.4	3.4	0.3	0.2	
	C	3	78.7	12.7	0.3	0.2	65.7	8.4	2.2	1.9	—	—	3.8	1.1	1.0	0.5	3.2	1.1	1.3	0.6	
	D	5	28.1	3.8	1.2	0.3	11.3	2.4	1.0	0.3	—	—	2.8	0.6	0.3	0.1	2.6	1.4	5.7	0.8	
17 Oct	A	5	12.3	3.0	0.1	0.1	3.5	2.3	1.0	0.5	—	—	0.8	0.3	2.4	1.1	3.9	1.0	0.2	0.1	
	B	5	19.0	3.1	0.1	0.1	13.0	3.0	0.4	0.2	0.1	0.1	0.3	0.2	0.2	0.1	4.5	1.4	0.3	0.2	
	C	5	16.9	3.1	—	—	7.7	2.0	1.4	0.7	—	—	0.9	0.2	0.6	0.2	2.6	1.5	2.8	0.7	
	D	5	11.6	1.3	—	—	4.8	0.7	0.4	0.2	—	—	0.7	0.4	0.6	0.2	1.4	0.5	2.3	0.6	
2007																					
9 May	A	5	6.3	1.8	—	—	0.1	0.1	—	—	5.8	1.8	—	—	0.4	0.1	—	—	—	—	
	B	4	4.9	2.4	—	—	0.1	0.1	0.3	0.1	2.5	1.4	—	—	1.0	0.4	—	—	0.3	0.1	
	C	5	4.2	1.1	—	—	0.2	0.2	—	—	0.5	0.2	0.1	0.1	2.9	0.8	—	—	0.0	0.0	
	D	5	1.8	0.9	—	—	0.1	0.1	—	—	0.2	0.1	0.2	0.2	0.5	0.3	0.6	0.6	0.1	0.1	
25 Jul	A	5	4.5	0.7	0.3	0.2	0.5	0.3	0.1	0.1	—	—	0.3	0.1	1.0	0.2	2.0	0.4	—	—	
	B	5	5.7	1.1	0.2	0.2	3.6	0.6	0.1	0.1	—	—	0.5	0.3	0.3	0.1	0.5	0.2	—	—	
	C	5	25.3	4.3	0.3	0.3	18.2	4.2	0.8	0.3	—	—	1.3	0.3	1.3	0.4	0.8	0.3	—	—	
	D	5	21.0	7.0	—	—	17.7	5.6	0.5	0.2	—	—	0.4	0.2	0.3	0.1	0.1	0.4	0.4	0.4	
9 Oct	A	5	2.4	1.3	—	—	0.4	0.2	—	—	—	—	0.3	0.1	0.9	0.6	—	—	0.2	0.1	
	B	5	1.9	0.7	—	—	1.3	0.5	—	—	—	—	0.3	0.2	—	—	0.1	0.1	0.1	0.1	
	C	2	21.0	5.5	—	—	1.5	0.5	—	—	—	—	4.0	0.0	0.5	—	9.3	6.8	1.8	0.3	
	D	5	8.1	3.1	0.1	0.1	0.2	0.1	0.1	0.1	—	—	0.4	0.2	0.4	0.4	5.9	2.9	—	—	

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